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The Tissues of Some of the Plants of the Sotol Region

BY WILLIAM L. BRAY

The opening of the desert botanical laboratory of the Carnegie Institution at Tucson, Arizona, with its facilities for studying the environmental conditions and the life phenomena of desert vegetation, marks an appropriate time for beginning a revival of the study of the tissues of desert plants. During the period of great activity of the study of plant structures as related to environment, say, from 1880 to 1895, desert plants—at any rate xerophytic plants—were especially selected because of the very striking adaptive phenomena exhibited in their organs and tissues. The literature of the period abounds in noteworthy contributions to our knowledge of the structure of desert plants, and their means of adaptation to their environment, of which perhaps the most noteworthy was Volken's "*Flora der aegyptisch-arabischen Wüste*" (1887), although in the more general ecological works, such as Haberlandt's "*Physiologische Pflanzenanatomie*" (1884; ed. 2, 1896), Warming's "*Lehrbuch der ökologischen Pflanzengeographie*" (1896; original Danish ed., 1895) and Schimper's "*Pflanzen-geographie auf physiologischer Grundlage*" (1898), the structures of desert plants have supplied many of the most instructive and interesting examples in adaptation phenomena.

During this active period, the various ecological forms and the more numerous adaptation devices in xerophytes were described, so that for us there would now seem to remain little to say as to the effect of desert environment upon the form or habit of plants, and upon the structure of various tissues such as epidermal, assimilation, absorption, etc. As a matter of fact, however, very few of the ecological forms of our American desert vegetation have been embraced in a special physiologic-anatomical study, and besides, progress has been made, meanwhile, in the study of physiological processes in plants, so that it would appear reasonable to expect helpful results from a renewed study of tissues of desert plants in the light of the most recent physiological knowledge. If the vital phenom-

ena in such a type as the star-cactus (*Ariocarpus fissuratus*), for example, were under investigation, it is very certain that these could not be made fully clear without a very accurate and detailed knowledge of the machinery through which they operate, *i. e.*, the various tissue systems in the organism. It is in just the unique — in a sense pathological — types like this and various other Cactaceae, Yuccae, Agaveae and others that the study of vital processes will be keenest, and these also are just the types in which the study of the tissues from the physiological point of view gives the greatest zest.

Since the study is distinctly a physiologic-anatomical one, the classification of tissues on the basis of function will be the preferable one as indicated in Haberlandt (*l. c.*) — for example, assimilation tissue will embrace cells whose main function is that of carbon assimilation, regardless of whether they are morphologically the cortex of a stem or the mesophyl of a foliage leaf or the superficial zone in a leaf of a succulent type such as *Agave*. But it is always to be noted what morphological parts have become devoted to certain functions, as that of assimilation, since it is desired to know why the cells of certain topographical regions of a plant have been chosen for this or that function.

In the present instance a study has been begun upon the tissues of a few of the most specialized of the ecological forms occurring in the very arid or desert region of Trans-Pecos Texas — a region which in this and in a subsequent geographic-ecological paper is designated the "Sotol Country," because of the predominance of the Sotol or *Dasyllirion Texanum* upon the most characteristic parts of the region. From the breaks of the Devil's River westward across the Pecos and beyond to the front ranges of the Rocky Mountain system and far southward in Mexico, is a vast limestone region well advanced in the progress of erosion, consisting of high conical hills and long ridges or divides with even slopes and with wide draws leading finally into deep-cut canyons such as those of the Pecos and Rio Grande and numerous side branches. This great area is thickly strewn with coarser or finer limestone débris resulting from the weathering of the soft upper part of the formation. There is no rich soil-covering to hide the rocks, and the vegetation is the scant and open formation characteristic of

rocky steppes (Felsensteppen), in this case made up of Yuccaeae, Agaveae, Cactaceae and desert shrubs like *Covillea*, *Flourensia*, *Koeberlinia*, *Fouquieria* and various Mimoseae. That is the typical Sotol area. As a matter of fact, this kind of formation occurs on most other foothills and mountain slopes westward, and especially in the Great Bend region, whether the geological formation be limestone or not, so long as there is the unstable covering of stony débris.

It would not be accurate to class all such country as desert, although the Great Bend region is as much so as the Sahara itself; but it is all a region in which plant life is beset by extreme environmental conditions such as the following :

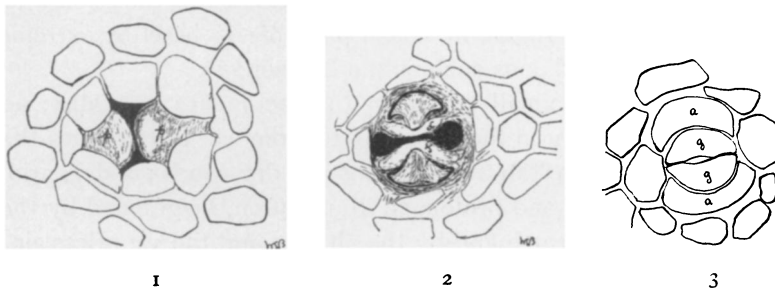
A precarious rainfall of fifteen to nine inches annually ; an evaporation capacity in the air equal to from six to ten times the annual precipitation ; strong and constant dry winds ; a dry, arid, stony soil ; intense and prolonged illumination, heightened by the glare of the stony earth and by the altitude and the vaporless air ; intense heating of the air, the stony earth and the plant bodies growing therein, in this respect approximating the maximum insolation endured by plant life in any region.

The species, of which only the tissues concerned in transpiration are described in this paper, were taken from the vicinity of Langtry on the Rio Grande near the mouth of the Pecos ; but all of them abound in the most extreme conditions of the Great Bend region and elsewhere.

1. *Agave Lecheguilla*. This is one of the less succulent-leaved agaves. The long, hard, spiny points of the leaves and their hard margins constitute a large proportion of mechanical tissue, the leaves being narrow and pike-formed because of the development of this tissue. The plant is, however, possessed of ample storage capacity for erecting a flowering stalk eight to twelve feet tall and one to two inches in diameter at base. The epidermis (*f. 4, cu*) consists of long, columnar cells with a heavy cuticular layer and great thickness of water storage cellulose like *Frankenia bracteata* of western Australia and the South African aloes. At the junction of the epidermis and the underlying assimilation tissue, the walls of each are rather thick, thus binding the two more firmly together and preventing the tearing loose of the epidermis

during the strain incident to alternate contraction and expansion. The cells of the assimilation zone are more or less palisade in arrangement and somewhat elongated, becoming interior-ward more nearly isodiametric and again thicker walled with numerous pits and large intercellular areas. Here, it is no longer assimilation but storage tissue.

The stomata are the specially interesting structures, naturally, since to them is entrusted the precarious function of opening a channel of communication from the external environment to the



Agave Lecheguilla.

FIG. 1. Surface view of stoma, showing the stomatal pit blocked by two projections *p, p*, fore and-aft.

FIG. 2. View of stoma shown in *f. 1* obtained by focusing on horizon immediately below 1. Projections from right and left block the passage by a compressed funnel-like structure (*f, f*) seen in cross-section in *f. 4*.

FIG. 3. The guard-cell apparatus lying below horizons 1 and 2. Obtained by removing thin tangential section of epidermis. *g, g*, guard-cells; *a, a*, auxiliary cells.

The orientation and magnification of the stoma is the same in the three figures.

delicate interior tissues, a fact equally true of each of the other species. The guard-cell apparatus of the stomata appears in surface view very much like that of numerous other Liliiflorae, the guard-cells proper being partially surrounded and held in place by the very much larger auxiliary cells (*f. 3*). But the protective apparatus above these is quite peculiar and different from any types with which the writer is familiar. Exterior-ward, where the stomatal pit opens upon the surface, two prominent projections of the epidermal walls fore-and-aft almost meet midway and block the passage except for two triangular entrances right and left (*f. 1*). Below this, two more complex projections from right and left again almost meet midway, leaving the merest slit at right angles

to the one above, and with two openings, this time fore-and-aft, and so alternating with the upper (*f. 2*). This inner arrangement is as if one were to take a rubber funnel and pinch the sides together midway (*f. 4, f, f*), leaving the margins otherwise flaring

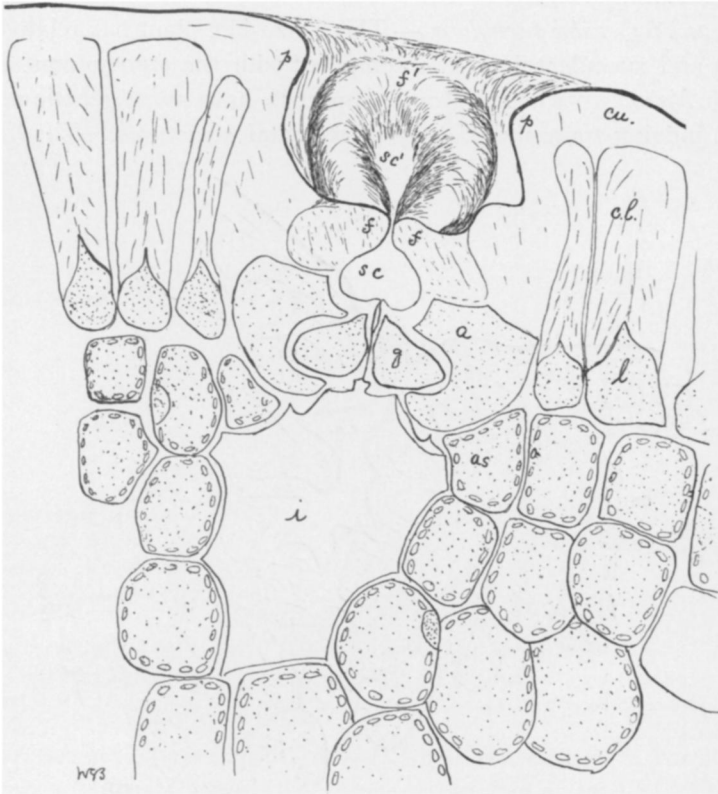


FIG. 4. Transverse section through superficial portion of leaf of *Agave Lecheguilla*. *cu*, cuticular layer of epidermis; *c.l.*, the cellulose layer; *l*, cell-lumen; *p*, rim of stomatal pit, which becomes a prominent projection above *f'*—the fore-and-aft projections seen in *f. 1*; *f, f'*, section of the inner projection with free margin at *f'*, the narrow median slit opening below into the still-air chamber, *sc*, which has wider communication through *sc'* (compare *f. 2*); *as*, assimilation tissue; *i*, the large, sub-stomatal air-chamber.

(*f. 4, f'*). Below the slit-like neck then, the tube of the funnel should expand bulb-like, thus representing the still-air space immediately over the guard-cell apparatus (*f. 4, sc*). Manifestly, such a device is well calculated to hinder direct communication

between interior and exterior and so fortify the plant against dangers entailed in such an exchange in so arid a climate. The air-chamber beneath the guard apparatus (*f. 4, i*) is relatively large and has ample connections by many channels with adjacent chlorophyll-bearing cells.

2. *Hesperaloe parviflora*.— This *Yucca*-like plant has relatively soft and succulent leaves as compared with the true yuccas, and with *Nolina*, to which it would appear to have some genetic relation judging from the identity of stomatal structures. The long

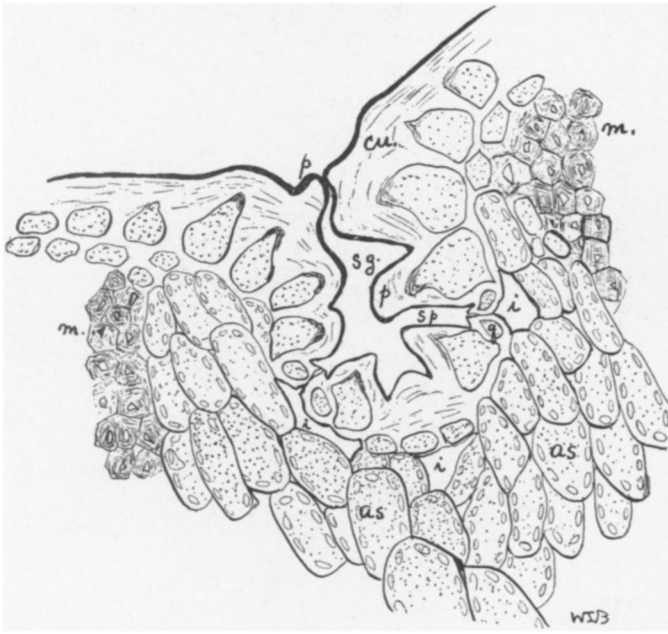


FIG. 5. Transverse section through superficial part of leaf of *Hesperaloe parviflora*. *sg*, stomatal groove; *p, p*, the blocking projections; *sp*, the stomatal pit; *m*, portion of bast-like mechanical rib; other abbreviations as before.

and rather slender and flexible leaves are longitudinally grooved and ridged, the grooves (*f. 5, sg*) providing a favorable location for the development of stomata, and the intervening ridges being ribs of bast-like, mechanical tissue (*m, m*). In the case of *Nolina* (*f. 6, m, m*) these ribs pass completely across the narrow diameter of the leaf, while in *Hesperaloe* they reach perhaps less than one third the distance across.

The rather deep grooves (*f. 5*, *sg*) widen out at the bottom, thus making a still-air chamber which is cut off from too free communication with the outside by the development of very numerous overlapping finger-like processes (*p*, *p*) equivalent to the hairy investment of stomatal pits in some plants. From the bottom and deeper sides of the groove, the stomatal pits proper (*sp*) descend through a thick epidermal wall to two very simply arranged and apparently rather immobile guard-cells (*g*) beneath which is an intercellular chamber (*i*) leading by various small channels to adjacent assimilation cells (*as*).

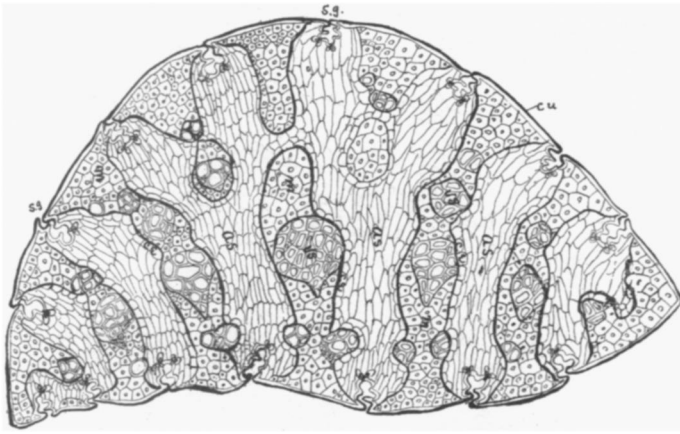


FIG. 6. Transverse section of leaf of *Nolina Texana*. *m*, *m*, girders of bast-like mechanical tissue enclosing the vascular conducting strands, *vs*, and alternating with bands of assimilation tissue, *as*; *ce*, sheath of non-chlorophyl-bearing (transportation?) cells investing the bast areas; other parts as above. $\times \pm 25$.

The assimilation tissue is, as one would expect, arranged with reference to the grooves, showing in cross-section a somewhat V-shaped zone of cells arranged along the sides of the groove and reaching from its bottom interior-ward to the apex of the V, gradually becoming isodiametric, thicker walled, storage-cells with much pitted walls.

3. *Nolina Texana*.—In the case of *Nolina*, the leaves are long, linear and grass-like, though rigid. They possess almost no storage tissue in the interior and the mechanical ribs extend across the leaf as girders (*f. 6*, *m*, *m*) separating the assimilation areas (*as*), which also reach across the thin diameter. Thus the

leaf is marked lengthwise by alternating bands of mechanical and assimilation tissue. The conducting tissue (*f. 6, vs*) is enclosed in the bands of mechanical bast-cells. In *Nolina* also the epidermis (*cu*) has very thick, rigid walls and plays an important part as mechanical tissue.

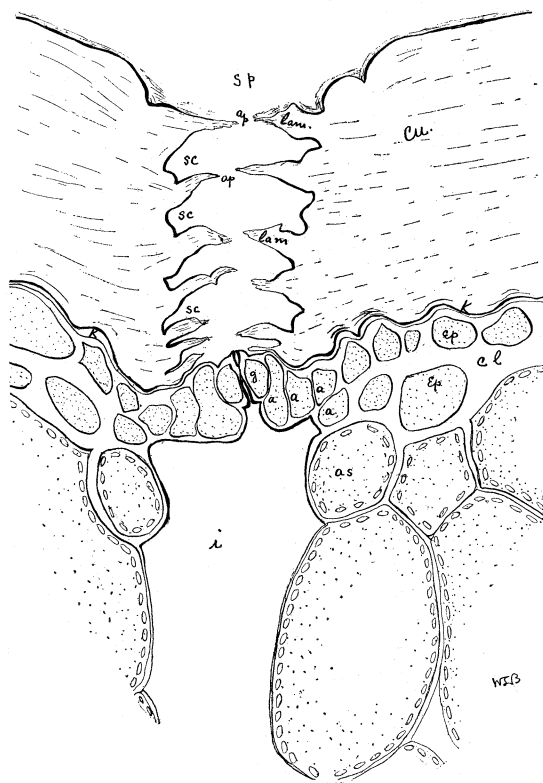


FIG. 7. Cross-section of epidermal region of *Ariocarpus fissuratus*, transversely through a stoma. *ep*, the double-layered epidermis with heavy binding wall, *cl*, and greatly developed cuticular (chitin-like) layer *cu*; *sp*, the stomatal pit leading down to the guard-cell apparatus, *g*, *a*, *a*, *a*, and interrupted by numerous diaphragm-like outgrowths, *lam*, with apertures, *ap*, so placed as to make a sort of spiral; *sc*, the successive still-air spaces; *k*, line of rupture between cellulose and cuticular layers of epidermis.

4. *Ariocarpus fissuratus* (*Anhalonium fissuratum*) commonly called the star-cactus and living-rock cactus, has a fleshy turnip-shaped body growing almost hidden in the dry adobe and with the exposed part so dusty gray as to be difficult to distinguish

from the loose rocks among which it grows. This exposed part consists of numerous imbricated triangular-pyramidal horny lobes from the axils of the interior of which the flowers arise. These lobes display the assimilation tissue and are in addition storage organs. The significance of the horny exterior is that of an external skeleton, which is the special need of a succulent body lying exposed to the crushing force of passing animals and shifting stones. This skeleton is so firm that the exposed part of the plant embracing the lobed portion retains its normal shape even after all the succulent part has disappeared from rotting, drying up or being eaten away by small animals. This chitin-like skeleton is a secretion of the epidermis which becomes many times as thick as the epidermal cells proper and is striated, showing the progressive thickenings (*f. 7, cu*). It is rather clear or like ground glass. Between the fissures and at the point of the lobes, this secretion is especially thick and horny. It is interesting to compare this tough epidermal secretion with that in the following type, *Euphorbia antisiphilitica*, which appears to arise in the same manner and is similarly striated, but is an easily frangible, soluble wax.

The epidermal cells proper are very small and form two irregular layers (*f. 7, ep*). This irregular arrangement together with the thick cellulose walls of these (*cl*) and the outermost assimilation cells, aids in binding the chitin-like layer more firmly. In spite of this, the whole skeletal covering becomes rather easily separated from the epidermal cells in the older parts (*f. 7, k*).

The stomatal opening is a very deep pit leading directly from the surface through the thick cuticle (*f. 7, sp*) to the guard-cell apparatus, the cells of which are in a depression somewhat below the general level of the epidermal layers (*f. 7, g, a, a*).

From the walls of the stomatal pit arise several stories of smaller outgrowths (*f. 7, lam*) stretched diaphragm-like across the pit, but perforated toward the center (*ap*) to allow the passage of gases. These perforations in the successive lamellae are so placed as to make a spiral zigzag passage for gases, from within outward or conversely. Not infrequently, a section shows a nautilus-like spiral of these lamellae and their apertures. By this remarkable device is the movement of gases hindered by a series of still-air chambers, and so excessive transpiration checked.

The guard-cell apparatus seems to consist of five or six pairs of auxiliary cells in addition to the usual guard-cells proper, giving a flexible arched covering to the large air-chamber beneath.

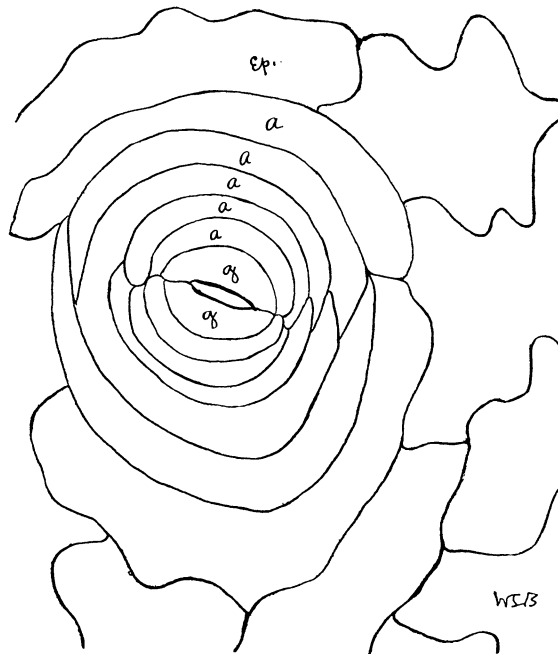


FIG. 8. Surface view of stomata like that shown in *f.* 7, after removing the cuticular layer. *g, g*, the guard-cells; *a, a*, etc., the five pairs of auxiliary cells; *ep*, the epidermal cells proper.

The cells of the assimilation zone are very large and arranged palisade-wise for several layers, becoming, then, spherical, thick-walled and much pitted storage-cells.

5. *Euphorbia antisiphilitica*. This is a leafless *Euphorbia* with the habit of an *Equisetum*. It occurs in very great abundance amongst the rocky débris of the hills and mountain slopes of the Great Bend region, especially in the Terlingua district, and is plentiful in some spots as far down the river as the mouth of the Pecos.

In general, the plant shows a moderately thick-walled epidermis thickly coated with wax (*f.* 9, *ep, wa*), which is clear and marked by minute longitudinal furrows on younger stems, but which be-

comes white and broken by fissures on the old stems. Beneath the epidermis is a thick zone of cortical assimilation perenchyma with cells elongated radially in the manner of palisade (*f. 9, as*). Toward the vascular cylinder, which, because of the great thickness of the cortex, appears to have the central location as in roots,

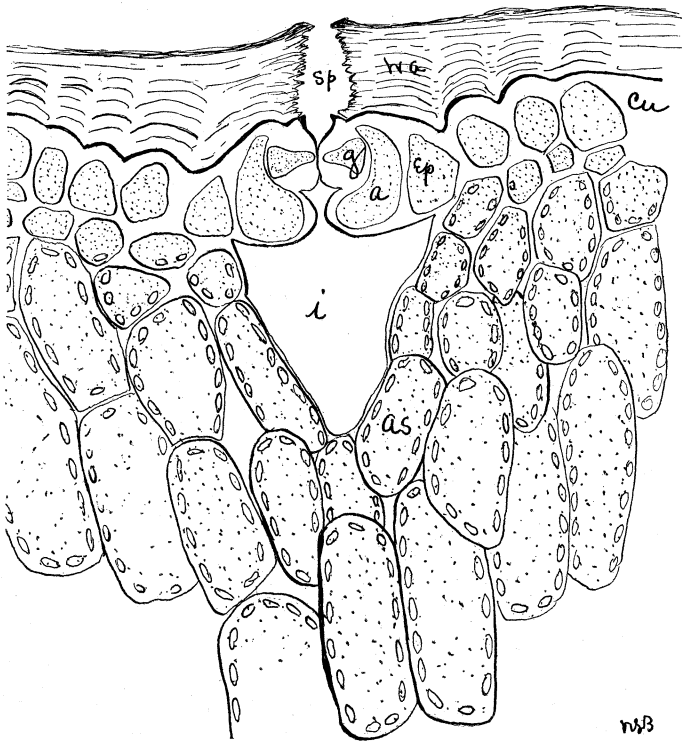


FIG. 9. Cross-section of young stem (1 yr.) of *Euphorbia antisiphilitica*, transversely through a stoma. *wa*, the heavy waxy secretion of the epidermis perforated at *sp*, by crater-like opening above the guard-cell apparatus, *g, a*; other lettering as before.

the assimilation-cells gradually become more nearly isodiametric, thicker-walled and pitted storage-cells. Within the vascular cylinder is an ample pith-region in which the cells are branched and disconnected so as to form almost a trabecular tissue (*f. 10, arm, i*).

Viewed from the surface, the stoma appears as a crater-like opening through the waxy covering, the wax being elevated about the pores, volcano-like. On younger stems it is easily observed that the stomata are more or less grouped or run in diagonal or

spiral clusters following certain wavy depressions in the stem. When the stem is perfectly turgid these depressions are faint, but with the approach of wilting they become more prominent. It appears that in this emergency the stomata would be depressed farther below the surface. Very interesting is it to examine a

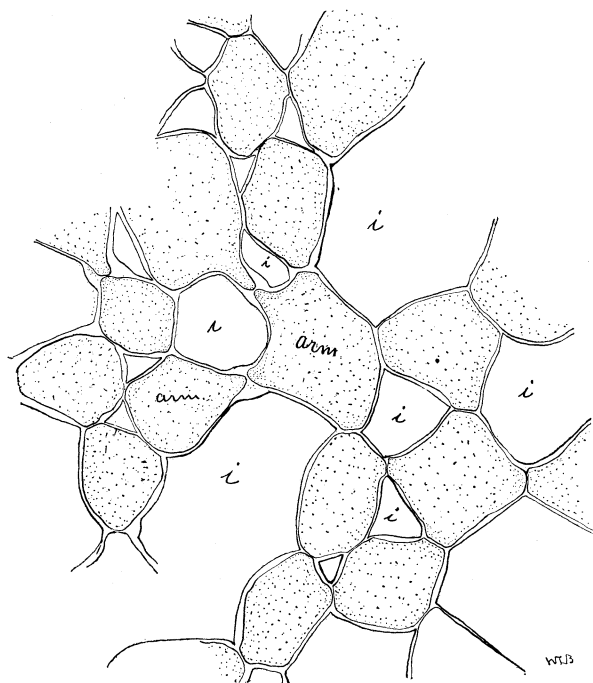


FIG. 10. View of portion of pith-area seen in cross-section of *E. antisiphilitica*; arm, the irregular pith-cells with numerous projecting arms giving lateral connection across larger or smaller intercellular passages, *i, i*, etc.

young wilted stem in which the stomata all lie at the bottom of the wrinkles caused by wilting. It would appear evident that the tissue beneath the stomata is less firm than elsewhere and as a matter of fact a superficial tangential section reveals that the sub-stomatal assimilation-cells are irregular, making 2, 3 or 4 way connections with other cells and so giving rise in effect to a limited spongy mesophyl.

The waxy covering appears to be a secretion of the epidermal wall. It is added layer by layer, the striations remaining distinct

(*f. 9, wa*) even when the covering is old and fissured. Structurally, there is much in common with the chitin-like cuticle of *Ariocarpus*, even the interruption at the stomatal pits showing a tendency of certain striae to continue across, diaphragm-like. It is distinctly waxy, however, and soluble in alcohol.

The epidermal cells themselves are small as in *Ariocarpus* and occupy about two irregular layers (*f. 9, ep*). Here, also, the walls of these and of the first underlying assimilation-cells (*f. 9, cu*) are notably thickened to give a firmer binding of the epidermis to the remaining tissues which the stress of alternating turgidity and flaccidity would tend to disrupt. The outer epidermal cells, at least, are ordinarily elongated with the stem-axis, but about the guard-cell apparatus they become box-shaped and more or less concentrically placed, forming a saucer-like depression at the bottom of which lies the guard-cell apparatus. The guard-cells proper are small and held in place above the ample air-chamber by two very large auxiliary cells which partially embrace the former (*f. 9, g, a*).

This stomatal structure recalls the case of *Euphorbia Tirucalli* of Zanzibar, figured by Haberlandt (*Physiologische Pflanzenanatomie, f. 162, 1896*), in which the appearance of young branches, the waxy covering, the stomatal apparatus and the crater-like openings in the wax above the stomata are all very similar to *E. antisiphilitica*, but Haberlandt's figure appears to be diagrammatic merely, since the waxy covering is not so conspicuously built up, but only a slight elevation above the general surface of the thick coat as shown in *f. 9*.

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